



A NEW ACTINOPTERYGIAN FISH  
FROM THE LATE PERMIAN OF THE PARANÁ BASIN, SOUTHERN BRAZIL <sup>1</sup>  
(With 5 figures)

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**ABSTRACT:** *Angatubichthys mendesi* gen. et sp. nov., an early actinopterygian fish from the Upper Permian of Paraná Basin (Corumbataí Formation), is described from four complete and articulated specimens preserved in a reddish siltstone obtained in an outcrop in Angatuba municipality, State of São Paulo. It is a small fish distinguished from the other palaeoniscoids by a combination of features: short and deep head; wrinkled median postrostral; nasal and dermosphenotic not in contact; suboperculum larger than operculum; conspicuous radiating ridges of ganoin on cleithrum and supracleithrum; longitudinal bands of ganoin on dentalosplenic; maxillary canal present; ethmoidal commissure on rostromaxilloantorbital; reduced number of branchiostegal rays; rows of deep smooth rhomboidal scales on flanks; and caudal fin heterocercal, deeply forked with almost equal-sized lobes. *Angatubichthys mendesi* gen. et sp. nov. appears to be more advanced than the so-called basal actinopterygians (*Cheirolepis*, *Mimia*, *Moythomasia*, *Polypterus*) due to various anatomical features (e.g., absence of pineal plate, presence of dermopterotic, deep scales on the flanks, presence of suborbitals, reduction of the number of branchiostegal rays, and reduced number of pectoral fin rays) but it wants synapomorphies of platysomid and neopterygian fishes.

**Key words:** *Angatubichthys mendesi* gen. et sp. nov., actinopterygian fish, Upper Permian, Paraná Basin.

**RESUMO:** Um novo peixe actinoptérgio do Neopermiano da Bacia do Paraná, Sul do Brasil

*Angatubichthys mendesi* gen. et sp. nov., um primitivo peixe actinoptérgio do Neopermiano da Bacia do Paraná (Formação Corumbataí), é descrito com base em quatro espécimes completos e articulados preservados em siltito avermelhado que aflora no município de Angatuba, Estado de São Paulo. Trata-se de um peixe de pequeno porte distinto de outros palaeoniscóides por uma combinação de caracteres: cabeça curta e alta; pós-rostral mediano de superfície enrugada; nasal e dermoesfenótico sem contato; subopérculo maior que o opérculo; conspicuas estrias radiantes de ganoína sobre o cleitro e supracleitro; faixas longitudinais de ganoína sobre o dentalo-esplênico; presença de comissura etmoideana e canal maxilar; número reduzido de raios de branquiostégios; fileiras de escamas rômbricas e lisas nos flancos; nadadeira caudal heterocerca profundamente bifurcada, com lobos de tamanho aproximadamente igual. *Angatubichthys mendesi* gen. et sp. nov. parece ser mais avançado que actinoptérgios basais (*Cheirolepis*, *Mimia*, *Moythomasia*, *Polypterus*) devido a presença de vários aspectos anatômicos (e.g., ausência de forame pineal, presença de dermopterótico, escamas altas nos flancos, presença de suborbitais, redução do número de raios de branquiostégios e número reduzido de raios da nadadeira peitoral), mas carece de sinapomorfias para platissomídeos e neoptérgios.

**Palavras-chave:** *Angatubichthys mendesi* gen. et sp. nov., peixe actinoptérgio, Neopermiano, Bacia do Paraná.

## INTRODUCTION

The Brazilian Paleozoic paleoichthyofauna is relatively diversified but the record of well-preserved specimens is extremely meager (RICHTER, 1991; DIAS, 1995). Concerning the actinopterygian fishes, most of the specimens are represented by scales, bony fragments, and isolated teeth (e.g., RICHTER, 1985; MEZZALIRA, 1989).

Few studies were based on almost complete and articulated fishes (DUNKLE & SCHAEFFER, 1956; BELTAN, 1978; MALABARBA, 1988; RICHTER, 1991; SANTOS, 1991; DIAS, 1995; FIGUEIREDO, DIAS & COSTA-CARVALHO, 1998; VEGA, DIAS & RAGONHA, 1997; VEGA-DIAS, DIAS & RICHTER, 2000; and RICHTER, 2002) and most of these fossil material were obtained from the Brazilian portion of the Paraná Basin.

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SANTOS (1991) reported the occurrence of actinopterygian fishes for the Permian of the State of São Paulo. The material consists of a poorly preserved platysomid fish from the Tatuí Formation (see FIGUEIREDO, DIAS & COSTA-CARVALHO, 1998), and nearly complete palaeoniscoid fishes from the Corumbataí Formation. PETRI (2001) pointed out that the latter material is remarkable due to the quality of preservation and taxonomic novelty. Unfortunately, the late paleontologist Rubens da Silva Santos (1918-1996) passed away without formally describing it.

In this paper, we describe the ray-finned fish from the Corumbataí Formation originally reported by Silva Santos (SANTOS, 1991), comparing it with other South American taxa and briefly discussing its affinities.

#### GEOLOGICAL SETTING

The Paraná Basin is an extensive rock unit placed at the Central-Southeastern South America, covering part of the political territories of Brazil, Argentina, Uruguay, and Paraguay and encompassing an area of about 1,200,000km<sup>2</sup> (MILANI *et al.*, 1998). Sedimentation took place during the Paleozoic and Mesozoic, and the stratigraphic record ranges from the Late Ordovician to the Late Cretaceous (LAVINA, 1991).

The following stratigraphic groups are recognised in the Paraná Basin: Paraná (Devonian); Tubarão (Upper Carboniferous-Middle Permian); Passa Dois (Upper Permian); São Bento (Triassic-Jurassic); and Bauru (Jurassic-Cretaceous) (ALMEIDA & MELO, 1981; PETROBRAS, 1998).

SCHNEIDER *et al.* (1974) argued that the Passa Dois Group is composed in the southern Paraná Basin by the Irati, Serra Alta, Teresina, and Rio do Rasto formations, and in the States of São Paulo, Goiás, and Mato Grosso, by the Irati and Corumbataí formations.

In São Paulo, the Corumbataí Formation corresponds to the Serra Alta, Teresina, and Serrinha (in part) formations. It consists of mudstone, siltstone, and shale of dark grey colour in the basal portion and reddish in the top (SCHNEIDER *et al.*, 1974; ALMEIDA & MELO, 1981; MILANI, FRANÇA & SCHNEIDER, 1994).

The predominant climatic conditions during sediment deposition of the Corumbataí Formation were dry, with low rainfall, which gradually produced scattered water pools (RAGONHA,

1989a). The paleoenvironment was probably transitional from neritic to lacustrine (MILANI, FRANÇA & SCHNEIDER, 1994).

The fossil record of the Corumbataí Formation is rich in bryophytes, pteridophytes, gymnosperms, sponges, mollusks, crustaceans, reptiles, and fish remains (MENDES, 1952; FÚLFARO, 1970; MEZZALIRA, 1989). Regarding the latter, it is common to find stratigraphic levels with a considerable amount of disarticulated bones, dipnoan dental plates, petalodontid teeth, palaeoniscoid scales, xenacanthid and hybodontid remains, besides ctenacanthid spines and coelacanth teeth (RAGONHA, 1989b; TOLEDO, BRITO & BERTINI, 1997). At the moment, the palaeoniscoid fish *Tholonotus braziliensis* Dunkle & Schaeffer, 1956 is the only relatively complete and articulated vertebrate known from that formation (DUNKLE & SCHAEFFER, 1956).

#### MATERIAL AND METHODS

The fossil fish material herein studied consists of four specimens preserved in a reddish siltstone. All specimens are housed at the Paleozoological Collection of the Departamento de Biologia Animal e Vegetal of the Universidade do Estado do Rio de Janeiro and are referred in this paper by the abbreviation Pz.DBAV.UERJ followed by the catalogue number.

The specimens were mechanically prepared with sharp steel needles and consolidated with PARALOID 67 dissolved in ethyl acetate. Casts of the specimens were made using CAF 73 (a silicone rubber). The specimens and casts were coated with a smoke of ammonium chloride to enhance skeletal details for photographs. Observations were made using a binocular microscope Olympus SZ 40. Line drawings were made from magnified photographic prints.

The anatomical terminology mainly follows GARDINER & SCHAEFFER (1989). The scale series formula follows WESTOLL (1944): D/P, A, C1, C2, where, D is the number of scale series anterior to the origin of the dorsal fin; P, number of scales series anterior to the pelvic fin; A, number of scale series anterior to the anal fin; C1, number of scale series anterior to origin of the caudal peduncle and C2, the number of scale series anterior to the end of the epichordal lobe of the caudal fin.

As far as possible, problems concerning homologies are discussed along the text. The

proposed diagnosis is based on the unique combination of primitive and derived characters that, although not rigorously in accordance with cladistic principles, this allows the identification of individual taxa when autapomorphies are wanting (ARRATIA, 1997).

Anatomical Abbreviations – r and l are used before anatomical terms to indicate right and left side respectively. (ANG) angular; (APR) anterior postrostral; (AUP) pars autopalatina of palatoquadrate; (ba.s.) basal shield; (BBR) basibranchial; (BR.R) branchiostegal rays; (CH) ceratohyal; (CL) cleithrum; (CLA) clavicle; (DH) dermohyal; (DPAL) dermopalatine; (DPT) dermopterotic; (DSPH) dermosphenotic; (DSPL) dentalosplenic; (e.ps.a.) canal for efferent pseudobranchial artery; (ENPT) endopterygoid; (f.e.a.) fenestra exonarina anterior; (ep. f.) epaxial fulcra; (ethm.c.) ethmoidean commissure; (f.e.p.) fenestra exonarina posterior; (FR) frontal; (fr.f.) fringing fulcra; (HBR1) first hypobranchial; (HP) hypohyal; (iorb.s.c.) infraorbital sensory canal; (JU) jugal; (l.l.s.c.) lateral line sensory canal; (LA) lachrymal; (LEXS) lateral extrascapular; (LG) lateral gular; (md.s.c.) mandibular sensory canal; (MEXS) medial extrascapular; (MG) median gular; (MPR) median postrostral; (MX) maxilla; (mx.c.) maxillary canal; (NA) nasal; (OP) operculum; (p.pl.) posterior pit-line of parietal bone; (PA) parietal; (PAS) parasphenoid; (PO) postorbital; (POP) preoperculum; (pop.s.c.) preopercular sensory canal; (PSCL) presupracleithrum; (PT) post-temporal; (QJ) quadratojugal; (R+PMX+ANT) rostromaxilloantorbital; (S) symplectic; (SCL) supracleithrum; (scl.b.) sclerotic bone; (SO) suborbital; (SOP) suboperculum; (sorb.s.c.) supraorbital sensory canal; (st.c.) supratemporal commissure; (t) teeth; (t.c.) temporal sensory canal; (t.pl.) transverse pit-line of parietal bone; (v.pl.) vertical pit-line of quadratojugal.

#### SYSTEMATIC PALEONTOLOGY

Osteichthyes Huxley, 1880  
Actinopterygii Woodward, 1891  
Actinopteri Cope, 1871  
Family indeterminate

*Angatubichthys* gen.nov.

Diagnosis – Fusiform palaeoniscoid fish of small size recognised by the following combination of features: head length contained about five times

in the maximum body length; short and obtuse snout; operculum smaller than suboperculum; broad and spatulate median postrostral, ornamented with delicate rugae on the anterior border; ethmoidean commissure included into the rostromaxilloantorbital; maxillary canal present; nasal separate from dermosphenotic; presence of dermopterotic; circumorbital ring including postorbital, jugal, lachrymal and two suborbitals; lanianiform teeth on the oral border of jaws; six branchiostegal rays; subequal medial and lateral extrascapular bones; suspensorium vertically inclined; post-temporal and cleithrum ornamented with conspicuous ridges; presupracleithrum present; dentalosplenic ornamented with fine longitudinal ridges; endopterygoid separated; pectoral fin twice as long as the pelvic fin; rows of smooth rhombic scales along the lateral side of the body, anteriormost ones three times as high as long; caudal fin heterocercal with almost equal-sized lobes; fin-rays closely articulated and fulcra are present along the leading edges of all fins.

Type-species – *Angatubichthys mendesi* sp.nov.

Etymology – A combination of the name of the type-locality (Angatuba) and the Greek word, *ichthys*, fish.

*Angatubichthys mendesi* sp.nov.  
(Figs.1, 2a, 2b, 3-5)

Diagnosis – As for the genus (by monotypy).

Holotype – Pz.DBAV.UERJ 059, a complete specimen, 66mm maximum length (ML); Westoll Formula (WF): 26/11, 20, 39, 53.

Etymology – The specific epithet is in honor of the late Brazilian paleontologist Josué Camargo Mendes, from the Instituto de Geociências of the Universidade de São Paulo, Brazil, who collected the material.

Additional material – Pz.DBAV.UERJ 60, complete specimen, 93mm ML [WF: 27/11, 20, 41, 57]; Pz.DBAV.UERJ 61 a (part) and b (counterpart), incomplete specimen, 57,9mm estimated ML [WF: 27/12, 21, 38, 5]; Pz.DBAV.UERJ 58, complete specimen 37mm ML.

Horizon and type-locality – Upper third of the Corumbataí Formation; Upper Permian (Kazanian). The outcrop is located between kilometres 200 and 210 of the Raposo Tavares Highway (SP-270), about 6km south of the municipality of Angatuba, São Paulo State.

## DESCRIPTION

*Angatubichthys mendesi* (Fig.1) reaches about 90mm of maximum length. The body is elegantly fusiform, laterally compressed and elongate, appearing to be subtrigonal in transverse section. The head is slightly longer than deep and the orbit is situated well forward. The cranium is brachycephalous and the dorsal profile is almost straight. The snout is obtuse, not projecting beyond the mouth opening. The dorsal fin is situated nearer to the caudal fin than to the head and its origin is approximately opposite to origin of the anal fin. The pelvic fin originates at about midway point between the pectoral and pelvic fin bases. The lateral line runs along the middle line of the body. There are 38 to 41 rows of rhombic and macromeric scales ahead of the hinge-line.

Most of the dermocranial bones have smooth surfaces, but show conspicuous growth lines apparently corresponding to concentric accretions of ganoin on the borders. Only rostromaxilloantorbital, median postrostral, dentalosplenic, and the bones of the pectoral girdle are ornamented conspicuously. The sensory canals are totally included in dermal bones and exit on the surface through minute pores.

The snout region is composed of the following bones: median postrostral, anterior postrostral, rostromaxilloantorbital, and nasal. The median postrostral (Figs.2b, 3-4; MPR) is a large spatulate bone forming most of the snout anterior to the orbit. This bone is long, about one third of head length. It lacks teeth and tubercles, but is ornamented with rugae on the anterior portion. In addition, there

are marked growth lines near the borders. The obtuse posterior border meets the frontals through an oblique and straight suture.

This bone meets the nasals laterally and the rostromaxilloantorbital anteroventrally. There is in its anterior third a lateral notch corresponding to the anterior limit of the fenestra exonarina anterior (Figs.2b, 3; f.e.a.).

In Pz.DBAV.UERJ 059 there is a small anamestic and reniform bone, slightly displaced from its anatomical position and lying anteriorly and below the median postrostral above the rostromaxilloantorbital. It was interpreted as an anterior postrostral (Fig.2b; APR). Probably this bone lies on a shallow depression between the anterior margins of the median postrostral and nasal. Its presence is not a regular feature in the specimens observed. This bone was observed by DUNKLE & SCHAEFFER (1956) in *Tholonotus braziliensis* and apparently corresponds to the lat-rostral of *Cheirolepis canadensis* Whiteaves, 1881 (see ARRATIA & CLOUTIER, 1996).

Presence of supranumerary bones in the rostral region is considered to be a primitive condition for actinopterygian fishes since it also occurs among sarcopterygian fishes and in the primitive *Cheirolepis* Agassiz, 1835. Therefore, the condition found in *Angatubichthys* (i.e., reduced number of bones in rostral region) is derived.

The rostromaxilloantorbital (Figs.2b, 3; R+PMX+ANT) is a small bone that forms the anterodorsal limit of the mouth opening. It is a complex and squarish bone, articulated dorsally with the median postrostral and nasal, and

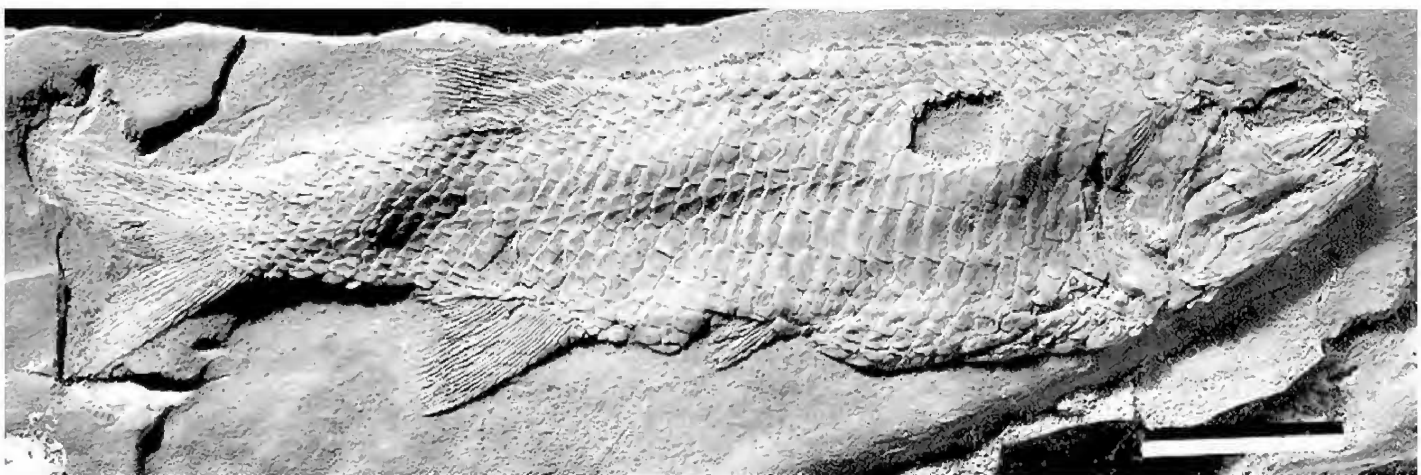
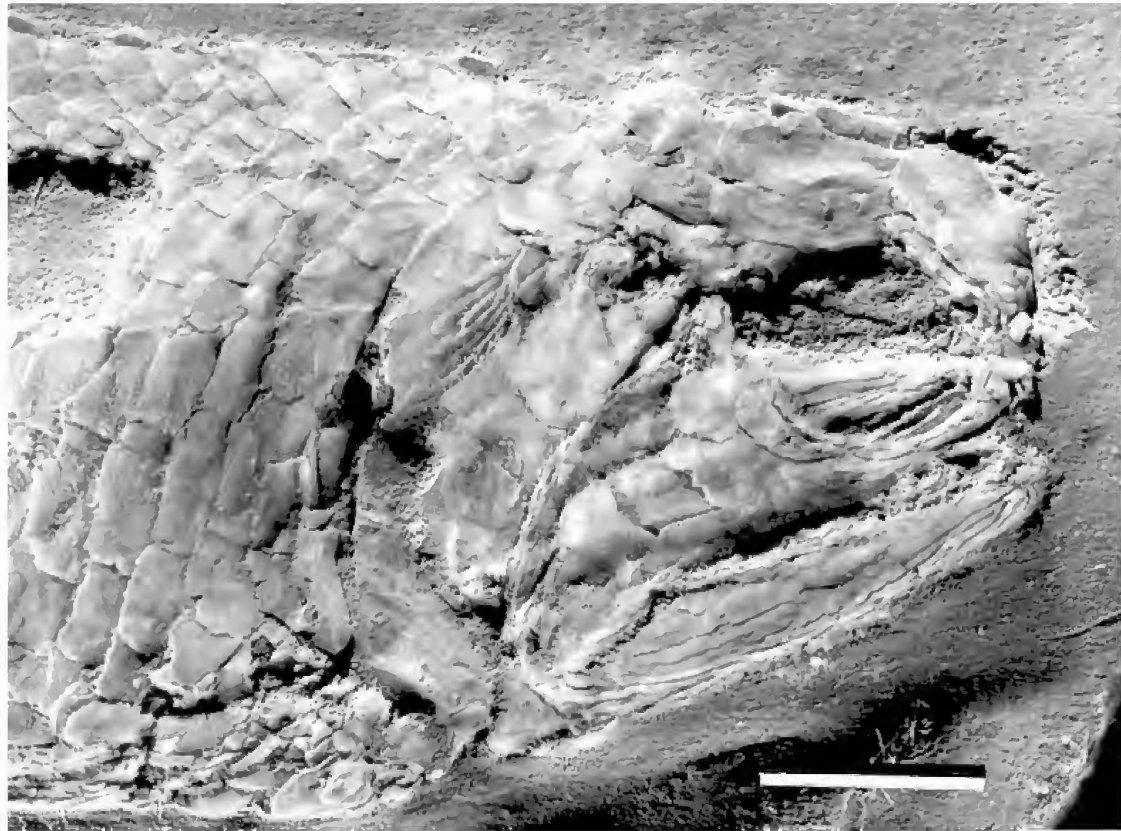


Fig.1- *Angatubichthys mendesi* gen. et sp.nov. Holotype (Pz.DBAV.UERJ 059). Scale bar = 1cm.

A



B

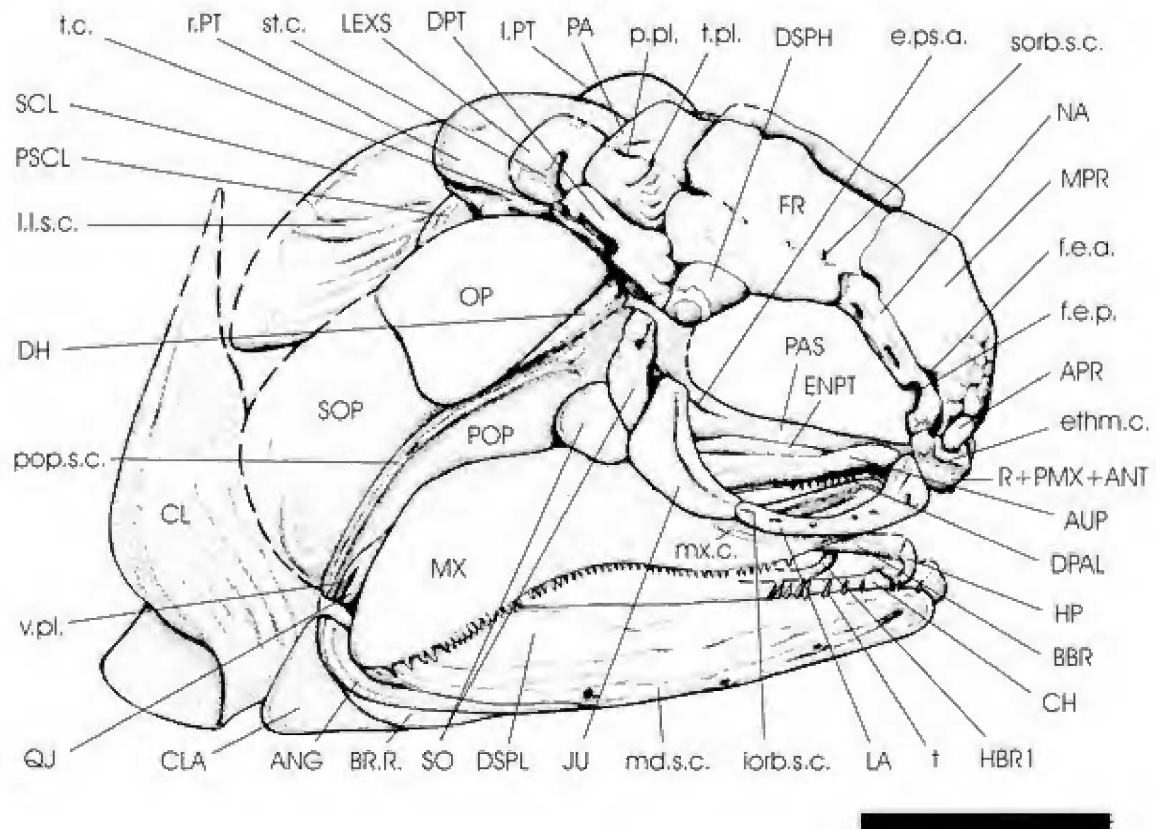


Fig.2- *Angatubichthys mendesi* gen. et sp.nov., skull of holotype (Pz.DBAV.UERJ 059): (A) photograph; (B) line drawing of A. Scale bar = 0.5cm.

posteriorly with the lachrymal above and maxilla below. It possesses a well developed neurodermal component marked by a tripartite pattern of sensory canals. The supraorbital and infraorbital sensory canals join together into the middle portion of the bone producing a well developed ethmoidean commissure (Figs.2b, 3; ethm.c.). The shape and arrangement of the bone correspond to that of *Rhadinichthys fusiformis* Lund & Poplin, 1997 (see LUND & POPLIN, 1997; POPLIN & LUND, 1997). In the holotype, there are in the oral margin of the rostromaxilloantorbital three round teeth-like structures, but we are unable to establish hitherto if they are true teeth or tubercles.

The nasal (Figs.2b, 3-4; NA) is a paired bone, straight and elongate, with length equal to that of the frontal. It meets the whole lateral margin of the median postrostral forming the anterodorsal limit of the orbit. It is inclined in relation to the basicranian axis meeting the frontal posteriorly through a limbate suture. The anterior third is capitate and in this region there is a notch corresponding to the posterior border of the fenestra exonarina anterior. In the orbital margin, another notch occurs, deeper than the anterior, for the fenestra exonarina posterior

(Figs.2b, 3; f.e.p.). The supraorbital sensory canal runs along the bone in the midline exiting on the surface through few minute pores. In *Cheirolepis* the nasal is divided into two bony elements. This condition is considered primitive to basal actinopterygians (POPLIN & LUND, 1995) whereas the condition of *Angatubichthys* is derived.

The frontal (Figs.2b, 3-4; FR) and postrostral are the largest bones of the skull roof. The frontal is subrectangular, with the longitudinal margins approximately parallel, and length equivalent to the orbital diameter. It is also wide, reaching the greatest width, near the dermosphenotic bone. Its width is about  $\frac{2}{3}$  of its length.

The posterior margin of the frontal is slightly wider than the anterior. Posterodorsally, it meets the dermosphenotic, posteriorly with a small portion of the dermopterotic, and medially with its antimere. The bone slightly overlaps the anterior margin of the parietal bone. A rounded medial projection in the middle third of the bone shows that this bone was slightly asymmetrical in some individuals.

The supraorbital sensory canal (Figs.2b, 3-4; sorb.s.c.) runs the frontal totally bone enclosed, exiting on surface through at least three large pores.

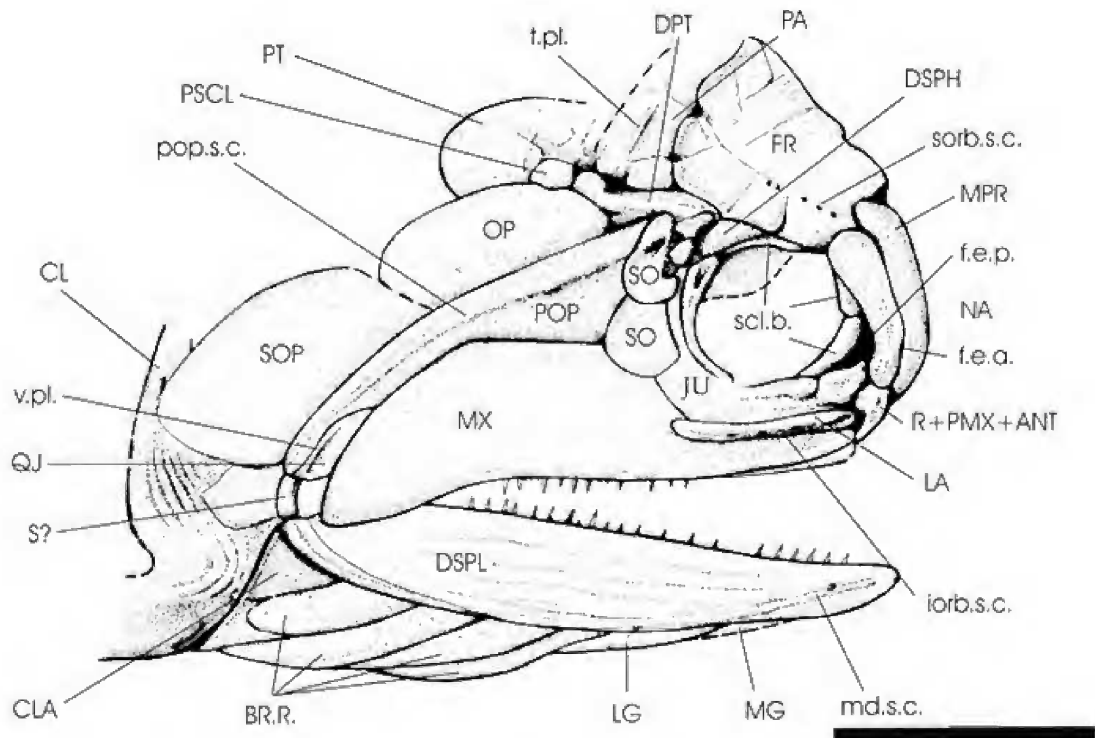


Fig.3- *Angatubichthys mendesi* gen. et sp.nov., skull of Pz.DBAV.UERJ 60. Scale bar = 0.5cm.

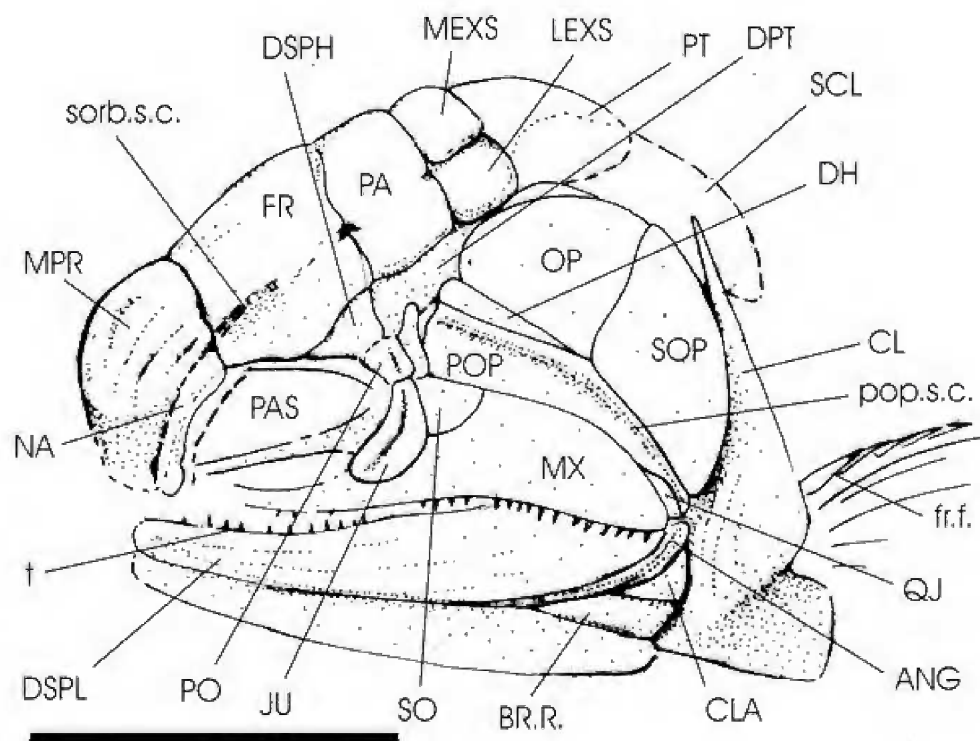


Fig.4- *Angatubichthys mendesi* gen. et sp.nov., skull of Pz.DBAV.UERJ 58. Scale bar = 0.25cm.

The frontal possesses a well-developed cleft, followed by a deep depression, in its posterior margin, corresponding to the projection of the supraorbital sensory canal into the parietal. This bone forms most of the dorsal margin of the orbit, separating the nasal from the dermosphenotic, as in *Polypterus* Lacepède, 1803, *Calamoichthys* Smith, 1865, and *Cosmoptychius* Traquair, 1877 and many other actinopterygians. Supraorbital bones are lacking.

The parietal bone (Figs.2b, 3, and 4; PA) is a paired and subquadrangular bone, about 1.5 times wider than long and 2.5 times shorter than the frontal. The lateral border is twice as long as the medial. Its surface is smooth, except near the anteroventral border, where there are conspicuous cuneiform striae. In the central portion of the bone there is a pair of pit-lines: an arciform transverse (Figs.2b, 3; t.pl.) and, a posterior one, running longitudinally in relation to the main body axis (Fig.2b; p.pl.), almost at right angle with the first. An anterior pit-line is lacking.

The parietal meets the dermopterotic laterally. Posteromedially, it joins the medial extrascapular and posterolaterally, the lateral extrascapular.

In *Cheirolepis* and in most of the sarcopterygian fishes, the parietal is a long bone, about the same length as the frontal. This condition is considered primitive to ray-finned fishes (POPLIN & LUND,

1995; ARRATIA & CLOUTIER, 1996). *Angatubichthys* and most of advanced actinopterygian fishes present derived condition.

The dermosphenotic (Figs.2b, 3, and 4; DSPH) is a small triangular bone that forms the posterodorsal limit of the orbit. The loop of the temporal sensory canal (otic branch) runs along the bone towards the postorbital. In most of the primitive actinopterygians there is an ypsiloid dermosphenotic. In *Angatubichthys*, the long orbital branch and the posterior process are lacking.

Medially, the dermosphenotic bone meets the frontal and posteriorly, the dermopterotic. In Pz.DBAV.UERJ 061 there is a gap between the dermosphenotic and the jugal, which is occupied by a postorbital bone.

The dermopterotic (Figs.2b, 3-4; DPT) is a subrectangular bone approximately three times as longer than wide. It forms the main part of the lateral border of the skull roof. The longitudinal margins are approximately parallel, except for the anterior third where the bone is wider and shows a crenulate border to the dermosphenotic and the frontal bones. A small space anteroventrally placed above the dermohyal is interpreted as a spiracular region. The temporal sensory canal pierces the bone along its longitudinal axis close to the lateral border.

Direct evidence from embryology of certain extant actinopterygians (*e.g.*, *Polypterus* Lacepède, 1803; *Polyodon* Lacepède, 1797; *Acipenser* Linnaeus, 1758; and *Amia* Linnaeus, 1766) shows that fusion of intertemporal with supratemporal occurs during early ontogeny (PEHRSON, 1922, 1940, 1944, 1947; JOLLIE, 1980, 1984; GRANDE & BEMIS, 1998) and this condition is considered derived for basal actinopterygians (GARDINER & SCHAEFFER, 1989). Based on that, a compound dermopterotic bone occurs in *Angatubichthys*.

There is a pair of subcircular extrascapulars, median and lateral, lying on the posterior limit of the skull roof. They are of same size, laminate and flat. The lateral extrascapular (Figs.2b, 3-4; LEXS) bears a tripartite outline due to the passage of sensory canals. The main sensory canal of the lateral line (Figs.2b, 3-5; l.l.s.c.) pierces this element producing a supratemporal commissure (Fig.2b; st.c.). It pierces the bone transversely crossing over to the medial extrascapular. Anteromedially, the lateral extrascapular meets the curved posterolateral border of the parietal bone and anterolaterally the dermopterotic. The lateral extrascapular also covers the anterolateral margin of the post-temporal bone.

Anteriorly, the medial extrascapular (Fig.4; MEXS) meets the parietal bone and laterally, the lateral extrascapular. Posteriorly, it overlaps the medial portion of the post-temporal bone.

The parasphenoid (Figs.2b, 4; PAS) is the only basicranial bone preserved. It is partially preserved in lateral view and can be seen within the orbit of the Pz.DBAV.UERJ 59 forming the floor of the anterior braincase. Laterally, it has a wing-shaped process that gradually tapers forwards. In the base of the ascending process there is a longitudinal groove for the pseudobranchial efferent artery (Fig.2b; e.ps.a.) as described by GARDINER (1973; fig.5, p.115; 1984) in *Mimia toombsi* Gardiner & Bartram, 1977 of the Gogo Formation, Australia.

The anteriormost portion of parasphenoid is laterally covered by the pars autopalatina of the palatoquadrate. The rest contacts the medial lamina of the endopterygoid bone.

There are fragments of an interorbital bony septum extending towards the parasphenoid in the posterodorsal corner of the orbit in Pz.DBAV.UERJ 059 and 060.

The anteriormost element of the circumorbital series, the lachrymal (Figs.2b, 3 LA), is a long and slightly arched bone occupying the

anteroventral corner of the orbit. Anteriorly, it is dilated, while slender rear.

The infraorbital sensory canal (Figs.2b, 3; iorb.s.c.) runs longitudinally through the median portion of the lachrymal. It is recognised on the surface of the bone by a delicate tubular inflated area and by the presence of at least three exiting pores.

Anteriorly, the lachrymal meets the rostromaxilloantorbital and posteriorly the jugal. The ventral border of lachrymal lies on a depression on the dorsal margin of the maxilla, hence the dorsal margin of the maxilla is partially covered.

The second element of the circumorbital series, the jugal (Figs.2b, 4; JU), is a crescent-shaped bone occupying of about  $1/4$  of the posteroventral corner of the orbit. Its membranodermal component is large and laminate. The infraorbital sensory canal pierces the bone close to the orbital rim.

The jugal meets the postorbital dorsally and posteriorly, the dorsal and ventral suborbitals.

The third element, the postorbital (Fig.4; PO) is a small, roughly trapezoidal bone only preserved in Pz.DBAV.UERJ 61. This bone forms with jugal, the posterior limit of the orbit. The infraorbital sensory canal pierces it dorsoventrally. The postorbital also occurs in sarcopterygians (SCHULTZE, 1993) and some basal actinopterygians (*e.g.*, *Pteronisculus magnus* Nielsen, 1942; see NIELSEN, 1942). The bone preserved in *Angatubichthys* is homochiral to that of *Pteronisculus* White, 1937.

The suborbitals (Figs.2b, 3-4; SO) are two anamestic dermal plates lacking ornamentation. The dorsal suborbital is a guttate and laminate bone. Anteriorly, it abuts the postorbital; ventrally, the ventral suborbital, and posteriorly, the preoperculum. The ventral suborbital is an ovoid bone, with a convex posterior border and anterior border almost straight. Anteriorly, it meets the jugal, ventrally the maxilla and posteriorly the preoperculum. Two suborbital bones occur in the most primitive actinopterygians (*e.g.*, *Mimia* Gardiner & Bartram, 1977; *Moythomasia* Gross, 1950), showing what it seems to be the primitive condition (GARDINER & SCHAEFFER, 1989).

There are four partially preserved sclerotic bones in the orbital region (Fig.3; scl.b.) of examined specimens. As in other paleoniscoid fishes, they are flimsy and arched structures.

The dermohyal (Figs.2b, 4; DH) is a triangular and elongate dermal bone, lying obliquely between preoperculum and operculum. It covers the lateral



face of hyomandibula near to the spiracular region. Apparently, the primitive condition for basal actinopterygians is to bear two dermohyals (or two antopercular bones) (GARDINER & SCHAEFFER, 1989). In this case, *Angatubichthys* presents derived condition in relation to *Cheirolepis* and *Moythomasia*.

The maxilla (Figs.2b, 3-4; MX) is a large bone, laminate and triangular. As in other paleoniscoid fishes it has a shallow and elongate anterior suborbital portion and a high and well-developed postorbital portion. Posteriorly, it is very inclined, covering part of the posterior end of the lower jaw. The oral margin contains lanariform teeth in the outer row and apparently delicate conical teeth in an inner row.

There is in Pz.DBAV.UERJ 059 a very reduced longitudinal sensory canal on the maxilla lying beneath the lachrymal bone. It is interpreted herein as a maxillary canal (Fig.2b; mx.c.) because of its resemblance with the feature occurring in the semionotid *Lepidotes elvensis* Blainville, 1818 (THIES, 1989).

The preoperculum (Figs.2b, 3-4; POP) is a malleiform bone consisting of a dorsal and well-developed subhorizontal arm and a ventral and slender vertical arm. The morphological pattern is similar to that of primitive actinopterygians such as *Mimia* and *Moythomasia* (see GARDINER, 1984). The dorsal arm is projected towards the orbit. Anterodorsally, it meets the dorsal suborbital and below the ventral suborbital. At the level of the posterodorsal angle of the maxilla, the preoperculum becomes narrow and vertical. This vertical arm ends before the posteroventral angle of maxilla. The preopercular sensory canal (Figs.2b, 3-4; pop.s.c.) runs close to the posterior margin of the bone. The subhorizontal arm of the preoperculum meets the dermohyal posteriorly, and, in part, the operculum. The posterior margin of the vertical arm articulates throughout its extension with the suboperculum.

The operculum (Figs.2b, 3-4; OP) is a sub-rectangular bone. The anterior border is straight and contacts the dermohyal. The posterodorsal margin is convex and the ventral margin shows a sigmoidal contact with the suboperculum. It partially covers the anterior margin of presupracleithrum, supracleithrum, and part of the lateral border of the post-temporal.

The suboperculum (Figs.2b, 3-4; SOP) is roughly trapezoidal and slightly larger than the operculum.

The posteroventral margin is more developed, covering most of the vast smooth inner lamina of cleithrum and meeting the posteriormost branchiostegal ray ventrally.

There are six branchiostegal rays (Figs.2b, 3-4; BRR) lying in series below angular and dentalosplenic. Ahead of the anteriormost branchiostegal ray there is a pair of gular plates. The lateral gular (Fig.3; LG) is triangular and slender in lateral view. An imprint in front of the lateral gular is interpreted as the median gular (Fig.3; MG).

The dentalosplenic (Figs.2b, 3-4 DSPL) is the largest bone of lower jaw. It is an elongate and shallow bone preserved with the ypsilateral angular, forming with it the outer surface of the lower jaw. Oral margin is almost straight and the ventral border slightly convex. Its greatest depth corresponds to about  $\frac{1}{5}$  of its length. Its anteriormost end is slightly rounded.

There are lanariform teeth (Figs.2b, 4; t) along the oral border of the dentalosplenic. In Pz.DBAV.UERJ 058A, interpreted as a young fish, apparently there is a double series of teeth. The inner series appears to consist of very small conical teeth, while more acuminate teeth form the outer. The dentalosplenic is densely ornamented on the outer surface with bands apparently corresponding to the sinuous accretion of ganoin. The mandibular sensory canal (Figs.2b, 3-4; md.s.c.) runs across the bone close to the ventral margin. From that, spaced and minute pores exit on surface.

The angular (Figs.2b, 3-4; ANG) is a fistuliform dermal bone that forms the posteroventral margin of the lower jaw. It typically carries in its midline the posterior section of the mandibular sensory canal.

The mandibular suspensorium is roughly triangular, large, and somewhat inclined. It is approximately as long as the maxilla. Considering shape and arrangement of preoperculum, the articular region between hyomandibula and otic endocranium is almost vertical. In Pz.DBAV.UERJ 059, the quadrate portion of palatoquadrate was partially preserved behind suboperculum. This portion appears to possess a large and convex articular area to lower jaw as in the acrolepid *Namaichthys schroederi* Gardiner, 1962. The contact zone with the lower jaw lies just behind the orbit. The design of the bones and their relationship with the parasphenoid follow the

pattern in *Australosomus kochi* Nielsen, 1949 (see NIELSEN, 1949).

The pars autopalatina (Fig.2b; AUP) of palatoquadrate is slender and narrow. Its anteriormost end is capitate. Most of the medial border abuts against the endopterygoid (Fig.2b; ENPT) that appears through the orbital space, as a narrow and elongate bone.

A dentigerous plate with pointed teeth meeting the ventral face of the pars autopalatina is interpreted as a dermopalatine (Fig.3b; DPAL). It is similar to that described by GARDINER (1962) in *Namaichthys schroederi*.

In Pz.DBAV.UERJ 060 the articular area of the palatoquadrate is poorly preserved, but among bone remains there is a nodular bone between ventral extremity of the vertical branch of preoperculum and the dorsal end of angular tentatively interpreted as a symplectic (S?, Fig.3). The presence of this bone among early actinopterygians is questioned by certain authors (GARDINER & SCHAEFFER, 1989) that claim this is a synapomorphy of Neopterygii. However, other (*e.g.*, OLSEN, 1984; VÉRAN, 1988) have been surveying anatomical evidences that indicate its early occurrence among primitive actinopterygians.

A small bone identified as quadratojugal (Figs.2b, 3-4; QJ) lies between the end of the vertical arm of the preoperculum and the posteroventral border of the maxilla. It is a triangular bone with a sharp dorsal extremity and a large base bearing conspicuous vertical pit-line (Figs.2b, 3; v.pl.). A vertical pit-line on quadratojugal was considered a relevant feature by BRITO (1997) to recognize that bone in various lineages of actinopterygians.

The following bones of the hyobranchial apparatus are preserved: dermohyal (seen above), ceratohyal, hypohyal, basibranchial, and hypobranchial.

The hypohyal (Fig.2b; HP) and the ceratohyal (= neocerato-hyal of VÉRAN, 1988; Fig.2b, CH) are partially preserved in lateral view in Pz.DBAV.UERJ 059. The first is a small triangular bone, slightly arched, with the round extremities synchondrally joined with the basibranchial plate. The second is seemingly a slender and long bone, but only its proximal capitate end can be seen.

Concerning the branchial apparatus, a basibranchial plate (Fig.2b; BBR) and the first hypobranchial (Fig.2b; HBR1) are preserved, in lateral view, in the gape of Pz.DBAV.UERJ 059. Both bones are somewhat elongate, the basibranchial being a wide and depressed plate and the hypobranchial slightly arched in the proximal portion.

The post-temporal (Figs.2b, 3-4; PT) is an ovoid and laminate dermal bone. The main sensory canal of the lateral line runs along a reduced portion of bone close to ventral margin. Anteroventrally, it is joined with the presupracleithrum and dorsoventrally with supracleithrum.

The presupracleithrum (Figs.2b, 3-4; PSCL) is preserved in all specimens. It is a small triangular bone lying on the anterodorsal corner of supracleithrum. Typically, it belongs to the pectoral girdle (see BJERRING, 1985) and not to the spiracular series as argued by certain authors (*e.g.*, LEHMAN, 1966). It occurs homoplastically in certain taxa of primitive actinops such as *Pteronisculus* White, 1937, *Paramblypterus* Sauvage, 1888, *Watsonulus* Piveteau, 1934, *Boreosomus* Stensiö, 1925 (*passim* LEHMAN, 1966).

The supracleithrum (Figs.2b, 3; SCL) is spatulate, well ossified and deep (1.8 times the height of the frontal and 1.2 times the height of the operculum). Ventrally, it is articulated with the dorsal process of the cleithrum. The bone is partially covered by operculum and suboperculum and is densely ornamented with radial ridges on the anterior margin. The main sensory canal of the lateral line crosses the supracleithrum obliquely, running from the anterodorsal region to the median point of the convex posterior margin of the bone.

The cleithrum (Figs.2b, 3-4; CL) is the largest dermal bone of the pectoral girdle. It is slightly sigmoid and typically bears a well-developed spine-shaped dorsal process. The portion below the spine-shaped process corresponding to the external lamina of the cleithrum is arched and ornamented with radial ridges. This rounded prominence covers the radials and the proximal portion of the lepidotrichia of the pectoral fin. It projects medially into a concave margin that is covered by the suboperculum. Its posterior margin is sinuous, convex below the spine-shaped process and concave ventrally. This last portion projects backwards in an outer lamina. The anteriormost part of cleithrum contacts the clavicle through an oblique suture.

The clavicle (Figs.2b, 3-4; CLA) is triangular and projected forwards; it is partially hidden by the posterior corner of lower jaw and branchiostegal rays. In primitive actinopterygians the clavicles are in close contact along the ventral midline. A narrow interclavicle is distinguished behind gulars (LUND, POPLIN & McCARTHY, 1995). In *Angatubichthys* we were not able to determine the presence of an interclavicle, probably because it is hidden by the

clavicle in all specimens examined.

The pectoral fin is directly associated with the cleithrum. It is relatively long, and the largest ray reaches the eighth scale row counting from the posterior margin of the cleithrum. It is approximately twice as long as the pelvic fin. It carries at least ten segmented and distally ramified rays. A reduced number of fin-rays (<25) in the pectoral fin is considered derived condition for basal actinopterygians (TAVERNE, 1997). Small and sharp fringing fulcra (Fig.4; fr.f.) are present along the leading edge of the fin.

The pelvic girdle is not visible. The pelvic fin is very small and triangular. Its base is relatively short; the length of the anterior margin corresponds to the half the length of anterior margin of anal fin. We counted at least 12 segmented rays. The pelvic fin is preceded by a modified subcircular scute.

The dorsal fin is triangular and moderate in size. The anterior margin is equivalent to the anterior border of the anal fin. The base of dorsal fin is approximately equal to the length of the anterior margin of pelvic fin. We count 21 segmented and distally ramified rays. The largest one bears about 11 articulate segments. Fringing fulcra occur on anterior border of fin preceded by at least three basal sagittate scutes. It was not possible to observe

any endoskeletal supports for the dorsal fin because it is hidden by rows of scales.

The anal and dorsal fins are placed at the posterior half of the body; the base of the anal fin is 1.5-2 times longer than the anterior margin of the pelvic fin. It carries at least 31 segmented and distally ramified rays. The anterior margin is covered with small fringing fulcra and the base is preceded by a small basal sagittate scute. Support elements were not observed.

The caudal fin (Fig.5) bears at least 50 distally ramified and segmented rays. In its dorsal margin there are 13-16 epaxial fulcra (Fig.5; ep.f.). They are long rod-like structures that progressively decrease in size toward the tail end. In the caudal base there are three basal sagittate scutes (Fig.5; ba.s.).

In the base of ventral hypochordal lobe there are two basal scutes and a series of small fringing fulcra (= "anterior lepidotrichia" of PEARSON & WESTOLL, 1979; fr. f., Fig.5).

The body is entirely covered with ganoid scales of smooth surface. In epaxial area scales are rhombic and equilaterals (4 longitudinal rows starting from back), the same for hypoaxial area (3 longitudinal rows up from abdomen). At the midline of body scales are higher than longer decreasing gradually in size backwards.

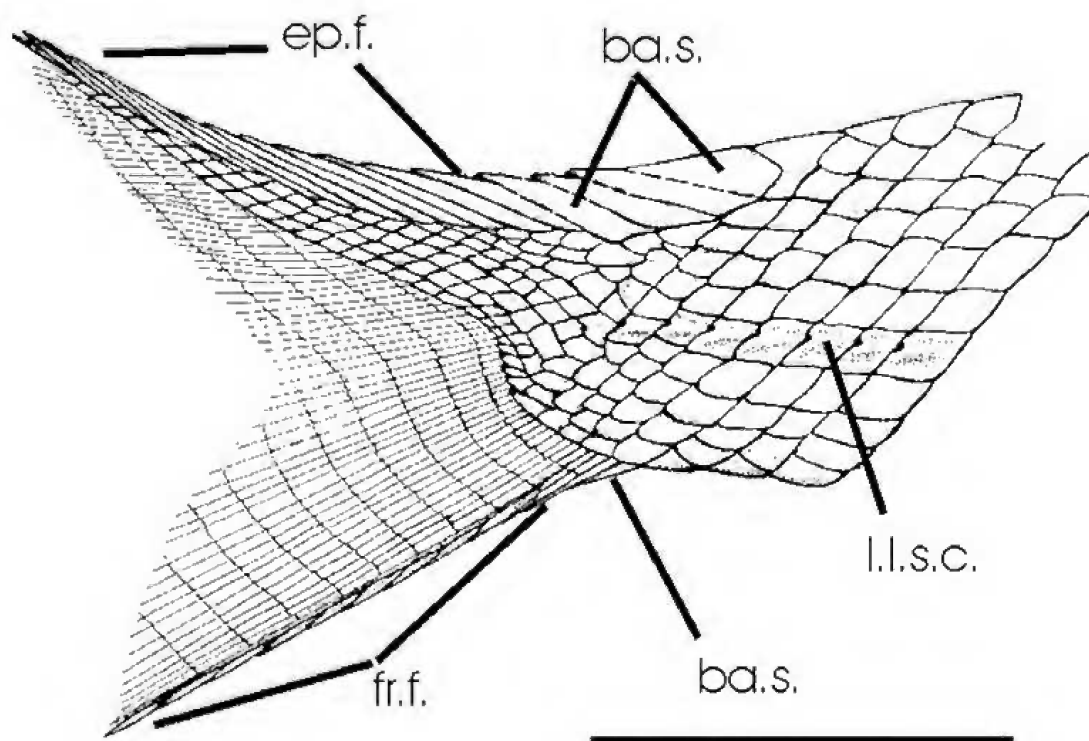


Fig.5- *Angatubichthys mendesi* gen. et sp.nov., caudal skeleton of holotype (Pz.DBAV.UERJ 59). Scale bar = 1cm.

The row of scales immediately above and two immediately below the lateral line are similar in size. Behind the pelvic fin the scales that compose these three rows gradually become equilateral toward hinge line, where they are small and elongated.

The lateral line scales are crossed at midline by the sensory canal which is totally enclosed. Their anterior and posterior borders show a moderately developed notch. There are about 38-41 middle flank scales, at least 30 of which are from lateral line. Anteriorly they are rhombic and deep and more equilateral near caudal peduncle.

Posterior to the hinge line there is a gradual change of direction and shape of scales in relation to the main longitudinal body axis (Fig.5). They become inclined and lozenge-shaped.

There are about 24 modified sagittal dorsal fin scales in the back, from the occiput to the origin of the dorsal fin.

#### DISCUSSION AND CONCLUSIONS

*Angatubichthys mendesi* and other South American palaeoniscoid fishes

Comparisons between *Anagatubichthys mendesi* and palaeoniscoid fishes previously described from Brazil on the basis of either nearly complete or well-preserved specimens, indicate that *Tholonotus braziliensis* (?Acrolepididae) shares an amount of general similarities. However, it can be distinguished from *Angatubichthys* by the presence of the following features: an arched dorsal profile (semionotid-like); large frontals with narrow anterior portion and excluded from the orbit; small postrostral; dermosphenotic obliquely truncated in its anterior portion, but with a posterolateral expansion; dermosphenotic covering the orbit and contacting the nasal; operculum larger than suboperculum; weak or absent dentition; pectoral and anal fins with 17 rays; dorsal fin placed in the middle of the body and anterior to anal fin; and scales ornamented with wrinkles.

*Tholonosteon santacatarinae* Beltan, 1978, is a large palaeoniscoid from the Upper Carboniferous of the State of Santa Catarina, about which few anatomical structures relevant to systematics are known, mainly due to the fact that skull is lacking. But this species can be easily distinguished from *Angatubichthys mendesi* by suitable features such as: an arched dorsal profile; 36 soft rays in pectoral fin; dorsal fin with base longer than deep, rising in

the middle of the body and composed of 25 rays; caudal fin deeply forked and bearing 68 rays, besides the presence of 20 dorsal scutes and scales along the body ornamented with delicate longitudinal rugae.

Additionally to describing *Tholonosteon santacatarinae*, BELTAN (1978) reported the occurrence of various species of palaeoniscoid fishes from the Upper Carboniferous of Uruguay based on partially complete specimens. Among those taxa, *Gondwanichthys maximus* Beltan, 1978 (Acrolepididae) and *Carbinolepis uruguayensis* Beltan, 1978 (Acrolepididae) promptly differ from *Angatubichthys* for their supranumerary extra-scapular and grooved scales; *Mesonichthys antipodus* Beltan, 1978 (Acrolepididae), for a fenestra exonarina anterior higher on snout and operculum larger than suboperculum; *Elonichthys macropercularis* Beltan, 1978 (Elonichthyidae), for the presence of ornamented scales, oval rostral and large number of branchiostegal rays (15); *Rhadinichthys rionigher* Beltan, 1978 (Rhadinichthyidae), for a dermosphenotic contacting the nasal and scales with parallel grooves; *Itararichthys microphthalmus* Beltan, 1978 (Pygopteroidea), for a reduced orbit, a single sclerotic bone, and supranumerary extrascapulars; *Daphnaecheilus formosus* Beltan, 1978 (Amblypteroidea), for skull higher than long, small or lacking rostral, operculum larger than suboperculum, and triangular and small parietal.

Furthermore, BELTAN (1989) erected two new monotypical palaeoniscoid families: Monesedeiphidae and Irajapintoseidae. The first includes *Monesedeiphus* Beltan, 1989, an aberrant palaeoniscoid recognised mainly for the presence of 15 extrascapulars and 12 branchiostegal rays, five suborbitals, and skull roof bones ornamented with tubercles and rugae of ganoin. The family Irajapintoseidae includes *Irajapintoseidon* Beltan, 1989, that possesses a robust postrostral with V-shaped posterior suture, nasal in contact with the dermosphenotic, operculum twice as large as suboperculum, 12 extrascapulars, and scales ornamented. Therefore, both differ considerably from *Angatubichthys mendesi* in various diagnostic anatomical features.

*Santosichthys mafrensis* Malabarba, 1988 (?Elonichthyidae) is known mainly from a skull cast. It differs from *Angatubichthys mendesi* mainly by the presence of a prominent snout; narrow frontals ornamented with rugae; long dermosphenotic forming a digitate projection towards the frontal; well-developed trapezoidal dermosphenotic forming the posterodorsal limit of the orbit; narrow and

slender maxilla; presence of supraorbital bone; high number of branchiostegal rays (16); and rhomboid scales ornamented with wrinkles and indented posterior border.

RICHTER (1991) pointed out the occurrence of eight new palaeonisciform fishes mostly from Santa Catarina State, not yet formally described. Examining restorations made by her, we are unable to find any remarkable similarities with *Angatubichthys mendesi*. The pattern of the dermal bones skull, particularly the non-contacting condition between nasal and dermosphenotic is enough to separate these fishes from *Angatubichthys*.

COX & HUTCHINSON (1991) pointed out the presence of an early actinopterygian fish to the Late Permian of Pedra do Fogo Formation: *Brazilichthys macrognathus* Cox & Hutchinson, 1991. It is represented by a poorly preserved cranium which can be distinguished from that of *Angatubichthys* by the presence of skull bones ornamented with ridges and tubercles, large maxilla with convex orbital portion, two rows of large teeth on maxilla and mandible, the inner row bearing stout and spaced fang-like teeth; unusual premaxilla, and nasal contacting dermosphenotic bone.

VEGA, DIAS & RAGONHA (1997) registered the occurrence of palaeonisciform fishes for the Rio do Rasto Formation, Permo-Triassic of the Paraná Basin, district of Santo Antônio da Platina, State of Paraná. The material consists of seven incomplete fishes preserved on the same bedding plane. In all specimens most of the skull bones are lacking, constraining an accurate identification. Three different morphotypes were described suggesting new taxa (VEGA-DIAS, DIAS & RICHTER, 2000). A high number of scale rows separate these taxa from *Angatubichthys*.

BORDAS (1944) reported the occurrence of the following species from the Triassic of Argentina: *Pseudobeaconia bracaccinii* Bordas, 1944 and *Pseudobeaconia elegans* Bordas, 1944 (Redfieldiidae), *Cleithrolepis cuyana* Bordas, 1944 (Cleithrolepididae), and *Mendocinichthys (=Mendocinia) brevis* (Bordas, 1944) (Perleidiidae). All these taxa share a deep body and arched dorsal profile as in various so-called "subholostean" fishes, therefore differing from *Angatubichthys mendesi*.

More recently, RICHTER (2002) described a complete palaeoniscoid fish from Late Permian of the State of Santa Catarina (Rio do Rasto Formation): *Rubius*

*pascoalensis* Richter, 2002. The fish possesses an anvil-shaped dermosphenotic meeting the nasal and the intertemporal does not reach the nasal. In addition, the operculum is larger than the suboperculum. These features are enough to separate *Rubius* Richter, 2002 from *Angatubichthys*. Other palaeoniscoid fishes were reported from the Paleozoic of the Paraná Basin. Some remains were tentatively identified as belonging to *Acrolepis* Agassiz, 1833 and *Elonichthys* Giebel, 1848 (BELTAN, 1978; RICHTER, 1985). However, these are based on fragmentary material consisting of isolated bones, scales, and teeth, limiting adequate identification and comparisons. But, *Angatubichtys mendesi*, when compared with well known oversea species of Acrolepididae and Elonichthyidae such as *Acrolepis sedgwicki* Agassiz, 1834 and *Elonichthys robisoni* Agassiz, 1843, shares only plesiomorphous similarities. Otherwise, the families Acrolepididae and Elonichthyidae, presumably represented in the Brazilian Paleozoic strata, are hitherto paraphyletic assemblages (GARDINER & SCHAEFFER, 1989). Their scales have been reported to get three times higher than long as in the flanks of *Angatubichthys mendesi*. It is probable that many scales assigned to taxa of these families belong to representatives of several non related groups.

The early actinopterygian scale structure is, in general, conservative (retaining many plesiomorphies). An attempt by ALDINGER (1937) to define groups based on certain patterns of canaliculi distribution and ornamentation have been recently questioned (GARDINER & SCHAEFFER, 1989, SCHULTZE, 1996; but see RICHTER & SMITH, 1995 for a new approach to assess scale features of actinopterygians). We assume that the current knowledge of the morphological diversity of scales is still in its infancy and will not allow a correct assessment of isolated scales of most of taxa.

Taking all of the current information about anatomy and systematics of South American palaeoniscoids there is little doubt that they are poorly known. Probably most of taxa form paraphyletic assemblages waiting for instant review. In addition, there is large amount of missing data to generate noise in a premature cladistic analysis. For similar reasons, *Angatubichthys mendesi* does not fit any species diagnosis within palaeoniscoid families described for the Paleozoic of Africa too (BROUGH, 1931; GARDINER, 1962, 1969; JUBB & GARDINER, 1975).

### Comments on the phylogenetic relationships of *Angatubichthys*

The most influent approach concerning phylogenetic classification of lower actinopterygian fishes is that by GARDINER & SCHAEFFER (1989). In order to tentatively place *Angatubichthys* in this system, the characters used by them are discussed independently, but not integrated into a cladistic analysis because of the large amount of missing data.

In this context, based on the available morphological data, *Angatubichtys mendesi* seems to occupy a more derived position in relation to various actinopterygians below the Chondrostei-Neopterygii divergence. For instance, the presence of dermopterotic bone (synapomorphy for the node H of GARDINER & SCHAEFFER, 1989, Fig.10) places it in a derived position in relation to assemblages such as “*Pteronisculus* group”, “*Boreosomus* group”, and “*Watsonichthys* group”. A reduced number of branchiostegal rays and a dermosphenotic contacting less than  $\frac{1}{3}$  of the dermopterotic (synapomorphies for the node I of GARDINER & SCHAEFFER, 1989, Fig.10) place it in a polytomy with a clade formed by “*Redfieldius* group” + “*Hoplolepis* group” and another, formed by “*Mesopoma* group” + (“*Aeduella* group” + (“*Platysomus* group” + (“*Bobasatrania* group” + “*Dorypterus* group”))). *Angatubichthys mendesi* lacks the skeletal apomorphies listed for the first clade (node J of GARDINER & SCHAEFFER, 1989, Fig.12), or for the second (node K of GARDINER & SCHAEFFER, 1989, Fig.12). It seems to be closer to the group where *Canobius* is included (“*Mesopoma* group”).

The “*Mesopoma* group” of GARDINER & SCHAEFFER (1989) that includes *Mesopoma* Traquair, 1890, *Canobius* Traquair, 1881 and *Styracopterus* Aldinger, 1937 is defined by the presence of an almost vertical suspensorium, reduced preoperculum, reduced posterodorsal processes of maxilla, suboperculum subequal or larger than the operculum, and T-shaped dermosphenotic (in *Mesopoma* and *Styracopterus*). No formal taxonomy was given for this group. Despite of general resemblances shared, only the presence of a suboperculum larger than operculum suggests putative relationship of *Angatubichthys* with taxa of this clade.

Unfortunately, due to the preservation of the specimens examined, the correspondence between the number of dermal rays and endoskeletal

supports of the fins, very important to clarify the systematic position of a fish as a stem actinopteran or a neopterygian (PATTERSON, 1982; COATES, 1999) was inaccessible to direct observation.

More recently, COATES (1999) tested the hypotheses of phylogenetic relationships for lower actinopterygians of GARDINER & SCHAEFFER (1989) including new anatomical data and additional taxa. The trees obtained are similar in various aspects to those of GARDINER & SCHAEFFER (1989). Most of the morphological features used in his analysis were observed in well-preserved specimens showing details of endocranium and brain. Such exceptional preservation is found in relatively few fossil taxa. Unfortunately, the available morphological data of *Angatubichthys* permits only comparisons of dermal elements of the skull, scales and fins.

In sum, the phylogenetic relationships of various taxa of lower actinopterygians have not yet been resolved. Considering an array of current phylogenetic approaches (KAZANTZEVA, 1971; KAZANTSEVA-SELEZNEVA, 1981; LONG, 1988; GARDINER & SCHAEFFER, 1989; LUND, POPLIN & McCARTHY, 1995; TAVERNE, 1997; COATES, 1998; 1999), *Angatubichthys mendesi* appears to be more advanced in relation to so-called basal actinopterygians (e.g., *Cheirolepis* Agassiz, 1835; *Mimia* Gardiner & Bartram, 1977; *Moythomasia* Gross, 1950; *Osorioichthys* Casier, 1952; *Howqualepis* Long, 1988; *Polypterus* Lacepède, 1803). It is suggested by several derived skeletal features (e.g., absence of plate pineal, presence of dermopterotic and suborbitals, high scales on the flanks, reduced number of branchiostegals and pectoral fin rays). Nevertheless, *Angatubichthys mendesi* wants synapomorphies of more advanced actinopterygian fishes of the platysomid and neopterygian clades.

It is hoped that additional informative specimens will allow the phylogenetic position of *Angatubichthys* and other lower actinopterygians from South America to be refined in the future.

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